Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

VOLUME XXXIII NUMBER 3

BOTANICAL GAZETTE

MARCH, 1902

THE RHEOTROPISM OF ROOTS.[1]

FREDERICK C. NEWCOMBE.

(WITH FIFTEEN FIGURES)

A. INTRODUCTION.

I. HISTORICAL REVIEW.

THE first author to write of the influence of streaming water in directing plant movement was Strasburger,[2] who worked with the creeping plasmodia of the Myxomycetes. Several years later Stahl[3] devoted some time to the consideration of the same subject. Jönsson,[4] however, the year before Stahl's paper appeared, published the first research on the behavior of roots in a stream of water. Jönsson used seedlings of *Zea mays*, *Triticum vulgare*, and *Secale cereale*, finding both primary and secondary roots bending their tips against the stream of water, attaining finally the horizontal position, no matter in what direction the roots were placed when first immersed. The author states that a similar result could be obtained with the roots of other species of plants, but he does not say what other plants he used, if any. Jönsson suspended his seedlings with their roots immersed in water conducted from a hydrant through a trough.

---

[1] XXXIII. Contribution from the Botanical Laboratory of the University of Michigan.

[2] STRASBURGER: Studien über das Protoplasma. Jenaisch. Zeitsch. **10**: 406. 1876.

[3] STAHL: Zur Biologie der Myxomyceten. Bot. Zeit. **42**: 145. 1884.

[4] JÖNSSON: Der richtende Einfluss strömenden Wassers auf wachsende Pflanzen und Pflanzentheile (Rheotropismus). Ber. Deutsch. Bot. Gesells. **1**: 512. 1883.

In 1896, I read before the American Association for the Advancement of Science a preliminary account of extensive experiments on the rheotropism of roots of seedlings. An abstract of this paper was published the same year in the BOTANICAL GAZETTE,[5] as well as in the *Proceedings* of the American Association for the Advancement of Science, and was briefly reviewed in the *Botanischer Jahresbericht;* yet it seems wholly to have escaped the attention of the two authors soon to be mentioned. In the preliminary account just cited, seventeen species of plants were reported, eight of them showing positive rheotropism, and nine showing no response to the streaming of the water. It was shown that definite relations exist between velocity of flow and response, that the latent period is influenced by various factors of the environment, that many roots are not responsive to a stream of water, that all roots which did respond were positive, that there are various degrees of sensitiveness in different species. Some attention was given to the nature of the stimulus, and it was suggested that it might be found to be pressure.

Very recently two authors have published papers on the subject of rheotropism. Berg[6] used the same apparatus that Jönsson employed, and another consisting of a basin of water in which he revolved seedlings fastened to a disk. By these means he found the roots of eleven plants to be positively rheotropic, while the root of *Glycine hispida* gave no response, though only three roots of the last species grew suitably for record. He devised a still better apparatus for securing streaming water; this consisted of a basin, to the water in which was given a rotary motion by a jet of water discharged in the basin in a tangential direction. Berg found the latent period of several roots at definite temperatures, and noted that the rheotropic curve began in the third or fourth millimeter zone from the apex of the root.

---

[5] NEWCOMBE: Rheotropism and the relation of response to stimulus. BOT. GAZ. **22**: 242. 1896; Proc. Amer. Ass. Adv. Sci. 1896; Bot. Jahresb. **24**^{1}: 74. 1896.

[6] BERG: Studien über Rheotropismus bei den Keimwurzeln der Pflanzen. Lunds Universit. Årsskr. **35**^{2}: no. 6. 1899.

Juel[7] made use of the same apparatus that I had described in my abstract in 1896 — a revolving basin of water in which the roots of seedlings were immersed. He worked with only three plants, *Zea mays*, *Vicia faba*, and *Vicia sativa*. The first two were found unsatisfactory, being irregular in their response, while the third was used for most of the results recorded. All three species were found to be positively rheotropic. No certain evidence for negative curving was found. The positive response for *Vicia sativa* was shown in velocities of current from 36^{cm} per second down to 0.3^{mm} per second. The maximum and minimum limits of velocity were not fixed. Juel experimented also with the location of the sensitive area, covering some root tips with collodion caps and decapitating some roots. In both cases he obtained responses in the streaming water, and concludes that the whole of the growing zone is sensitive ; whether the root-tip is sensitive was not determined. As to the nature of the stimulus inducing rheotropic bending, Juel could not decide. When he placed thin cylinders of collodion over his roots, the roots curved as before. He concludes that the stimulus may be pressure, but suggests that the collodion may have allowed a sufficient stream of water to pass through to give the same stimulus as when the root is naked.

It will be seen from the foregoing narration of work accomplished that there are various questions connected with rheotropism still unanswered. Some of these questions will be dealt with in the following pages. Especially will attention be given to the distribution of rheotropism among phanerogams, the sensitiveness of roots other than primary, the sensitiveness of roots of older plants, the relation of response to velocity of current, the latent period, the localization of the sensitive area, and the nature of the stimulus.

II. METHODS.

The majority of plants used in these experiments were seedlings. The seeds were planted in white pine (*Pinus Strobus*) sawdust. It was found that any other sawdust at hand would not give straight roots with several of the species. When the seedlings had attained a suitable length, they were removed from the sawdust, fastened to bars of white pine, and the bar was then suspended with the roots immersed in filtered tap-water. The method of fastening the seedlings to the wooden bar is so simple and so preferable to the common practice of pinning, that it may be worth while to illustrate it with *fig. 1*, and to detail it here. A bar of wood differing in diameter according to the size of the seedlings used is clamped in a vise. Two strips of heavy blotting paper are cut the same length and width of the wooden bar. Next, these two strips are dipped in water, and then laid, one covering the other, on the upper side of the wooden bar, and a rubber band is slipped on over one end of wood and blotting paper. The upper strip of blotting paper is raised with the fingers of one hand, while with those of the other a seedling is inserted between the two strips of paper and deposited close up to the rubber band. The upper strip of paper is then lowered upon the other, another rubber band slipped on, so that the seedling is held between the two pieces of blotting paper by two rubber bands, one on each side. The upper piece of paper is again raised, another seedling inserted, and so on till the bar is full.

---

[7] JUEL: Untersuchungen über den Rheotropismus der Wurzeln. Jahrb. Wiss. Bot. 34 : 507. 1900.

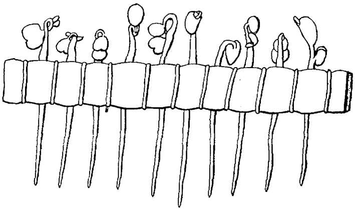

FIG. 1.—Seedlings of *Raphanus sativus*, illustrating the method of fastening to a bar of wood with blotting paper and rubber bands.

The great advantage of this method of suspending seedlings is seen in its avoidance of all trouble from Sachs's[8] curvature. The epicotyl or hypocotyl is left free to carry out this curve without changing the direction of the root. The simplicity and rapidity of preparation commend this method for various kinds of experimentation besides rheotropism. For seedlings whose roots are to be immersed in water, the blotting paper will supply a suitable amount of moisture, if it is allowed to touch the surface of the water. The wooden bar is wholly unobjectionable if of white pine. I have always taken the precaution of immersing these wooden bars for twelve or more hours in running water before using. I have tested a score of species of seedlings, and have never been able to discover any disturbance of growth having its source in the wood. A heavy bar of glass, with a plane surface for the seedlings might be substituted for the wood.

---

[8] SACHS: Arbeit. Bot. Inst. Würz. 1:402.

For many kinds of experiments in which roots are to be immersed in water, it is advisable, as here practiced, to allow the preparation to stand with the roots in water for twelve to twenty-four hours before beginning the experiment; for, with the seedlings of many plants, a few or many roots undergo curves or distortions when placed in water. In my experiments all roots which had deviated from the vertical direction were removed before the streaming of the water was begun.

In most of the experiments here recorded, a flow of water was secured by revolving glass basins full of water on horizontal klinostats and centrifuges. The centrifuges were turned for some experiments by water motors, and for others by an electric motor. The latter gave a constant rate of revolution, so that with it the effect of different velocities could be studied. The apparatus, except the motor, is shown in *fig. 2*. Juel states that in a similar revolving basin which he used, he found the current deviating from the tangential direction, due to the disturbing effect of the opposing roots. To overcome this difficulty he divided his large basin up into four concentric compartments by inserting glass dishes, one within the other. In the most of my experiments, I suspended my seedlings along but one diameter, while Juel suspended his along three diameters. There was more reason for irregular or cross-currents in his basin, therefore, than in mine. I have used basins subdivided into three concentric compartments, and others undivided, and obtained uniformly the same results with both. I made several tests by observing the movement of particles floating in my non-divided revolving basins, and assured myself that the flow as it met the roots was practically uniformly tangential. To avoid the disturbing effect of the light and change of temperature, the experiments were, in most cases, conducted in a dark room whose temperature was regulated to a variation of less than 2°. The lagging of the current was tested empirically by suspended and immersed particles, and found in all parts of the basin to amount to less than 1 per cent. in velocities of less than thirty revolutions per minute. In the data given in this paper this small retardation will be neglected.

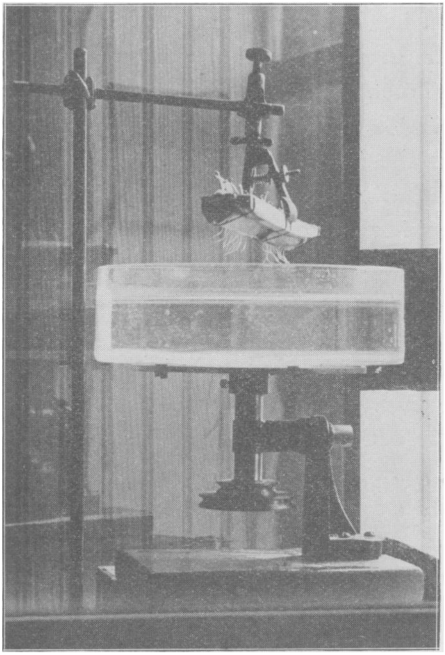

FIG. 2.—A centrifuge and a preparation of seedlings of *Brassica campestris* raised above the water. It will be seen that most of the roots show rheotropic curves of 45° or over, half of the curves being in one direction and half in the other, corresponding to the direction of the water-stream on opposite sides of the basin.

Besides the revolving basin, a narrow wooden trough was sometimes used. The water for this was obtained from a hydrant, and was passed through a gas-heater before being conducted to the trough. A few experiments were made during the night in a brook flowing through a deep ravine.

Various methods employed in the study of special parts of this problem would best not be given here; they will be found in the various sections of this paper.

III. GENERAL PHENOMENA.

The general appearance and progress of the phenomenon of rhetropism in roots are as follows: When plants rheotropically sensitive have their roots immersed in a current of water of suitable velocity, the roots bend with a greater or less angle against the stream, thus opposing the mechanical effect of the streaming water and the response to gravitation. The angle of curvature in this rheotropic response, as in other phenomena of irritability, is in the growing zone, and there is a definite latent period and after-effect. The angle of curvature in sensitive plants ranges from a few to 90°, thus bringing the tip of the root into the horizontal position. Rheotropism of roots is not a general phenomenon, and great variation in the degree of response is displayed by different species.

B. RESULTS WITH SEEDLINGS.

I. DISTRIBUTION AMONG PHANEROGAMS.

1. *Plants unsuited to experiment.*

Everyone who has made any considerable number of water cultures with seedlings has learned that various species or varieties produce in water only badly contorted primary roots. Obviously such plants cannot be used to any great extent in the study of rheotropism. *Zea mays*, in the four varieties of field and sweet corn employed, showed itself to be practically worthless for experiment with primary roots. The variety of field corn used was a *Western dent;* and of sweet corn, the *White cob*, *Early Minnesota*, and *Old colony*. One hundred and twenty-four individuals of these four varieties were grown in water till the main roots were from a few millimeters to 5^{cm} in length, and none of them produced in still water 30 per cent. of straight roots. In many cases the tip of the primary root was lifted above the water; in others, the root pursued a zigzag course downward; while in others the direction was an irregular spiral.

It is worth noting that Jönssen and Berg for the main part of their work used this erratic *Zea mays*, and Juel employed it to some extent. All three authors, however, call attention to the large number of contorted roots formed. My own results teach that the relatively small number of straight-growing roots of *Zea mays* (field and sweet corn) are feebly positively rheotropic.

Phaseolus vulgaris, *P. lunatus*, and *P. multiflorus* produce in water better roots than *Zea mays*, but still show a large percentage of contortion. It will be seen later on that these roots are not rheotropic.

Tropaeolum majus, *Pisum sativum*, *Vicia sativa*, and *Lathyrus odoratus* also produce many poor roots in water, though 40 per cent. to 80 per cent. will grow straight.

2. *Plants insensitive to a stream of water.*

Of the thirty-two species of plants tested for rheotropism, fourteen have shown themselves insensitive to the water-stream. These distribute themselves through nine families; while the rheotropic species number eighteen, and are distributed over six families. This result shows that rheotropism of roots is not a general phenomenon. In the narrative of experiments which is to follow, only those details will be given which are necessary to show the basis of the conclusions reached.

Three species of water plants, *Potamogeton perfoliatus*, *Elodea canadensis*, *Ranunculus aquatilis*, were brought under experiment, as follows: From vigorous individuals, apical portions were cut, 10^{cm} or more in length. These cuttings were secured in an upright position to thin glass rods, by tying with thread, and the glass rods were then fastened by rubber bands to a bar of wood 20^{cm} in length, which was suspended in the horizontal diameter of a suitable cylindrical glass aquarium containing water. The bar of wood was wholly above the water, and the lower parts of the glass rods with the plants were submerged. Several aquaria, thus prepared, were set in a south window, and the lower ends of the plants were screened from the direct rays of the sun. Within a week all plants had sent out several to many adventitious roots, the general direction of which was vertically downward. The preparations were then placed upon centrifuges, and the aquaria revolved, while the plants were held at rest in the vertical plane of a diameter. The glass rods and, to a greater extent, the plants themselves, necessarily disturbed the flowing of the water. But the plants were not more than five in any aquarium, and hence were well separated from one another. Moreover, after the disturbance in passing one radial row of plants, the stream had a full semicircle in which to compose itself before meeting the other radial row. A practical test, made by suspending algal filaments to the roots and watching their trailing, showed that the roots were met by a stream with a constant direction.

Five plants of Elodea were used, and these produced eleven roots in all. Two roots were in streams of a velocity of 628^{cm} per minute, not allowing for the lagging; two in streams of 345^{cm} per min.; and one in a stream of 162^{cm} per min. The revolution continued without interruption for 60 hours, and the temperature of the water varied from 24° to 28°. These eleven roots showed considerable nutation, but none gave any curve in response to the stream, the resultant position of each root being vertical.

Of *Potamogeton perfoliatus* four plants were used. The total number of roots formed was 48. They grew well in streams ranging in velocity from 200^{cm} per minute to 628^{cm} per minute. Constant revolution was maintained for 56 hours in a temperature varying from 24° to 28°, but no curves resulted. The roots were wholly indifferent to the stream.

Ranunculus aquatilis was represented by four individuals, which developed ten roots in all. The revolution continued for 72 hours in a temperature of 24° to 28° in water with the roots in a stream velocity of 188^{cm} to 284^{cm} per minute. The roots showed considerable nutation, but no curves in response to the stream. The nutation, like that in Elodea, consisted of oscillation through an arc often of 45° on each side of the vertical, but in the resultant the roots advanced straight downward, elongating several centimeters during the course of the experiment. In order to clear away any question that may arise at this point as to the suitability of the velocity of stream employed, it may be said that all of the plants which have shown themselves rheotropic have been sensitive to streams of the velocities given above.

From the results obtained with these three water plants, we may infer that rheotropism is not a general phenomenon with such plants. Possibly it may not be found in any water plant. It would seem to be of distinct disadvantage for such plants to be rheotropic in their roots. For only by insensitiveness to the flow of water can the roots the most quickly find the solid substratum.

Allium cepa was tested both in the bulb and in seedlings. The bulbs used were of the variety known as "multiplier." They were suspended so that the lower end dipped slightly into the revolving dish of water. Three periods of revolution were tried—9 hours, 24 hours, and 37 hours—with the temperature ranging from 16° to 23°, most of the time being above 20°. The velocities of flow ranged from 100^{cm} to 250^{cm} per minute. The number of roots growing well was twenty-eight, and these were most of them 2^{cm} long when the experiment began. In one of the three experiments eight roots bent positively, one negatively, and two grew vertically downward. In the two other experiments, one root bent negatively 90°, while the sixteen others grew in a vertical plane or showed no deviation caused by the current of water. It would thus seem that the roots from the bulb of this variety of the onion are either insensitive or at most but very slightly sensitive rheotropically. Twenty-three seedlings of the onion were tested in streams ranging from 75^{cm} to 600^{cm} per minute, there being continuous revolution for 38 hours, at a temperature of 23.5°. None deviated from the vertical direction, though all grew well.

Nasturtium officinale grows well with roots in water, all pursuing a remarkably straight course downward. Forty seedlings with roots 1^{cm} to 1.5^{cm} in length had their roots subjected to a continuous water stream for 45 hours, at a water temperature of 20.5° to 24.5°, velocity ranging from 100^{cm} to 900^{cm} per minute. All grew vigorously and vertically downward.

Ricinus communis also grows straight roots in water. Of the twenty-three seedlings used none curved in the water stream. Ten roots were in revolving water for 20 hours, and thirteen other roots for 48 hours, in temperature from 19° to 24°, in velocities from 150^{cm} to 1200^{cm} per minute, without one curve of any kind appearing.

Quercus alba was hardly sufficiently tested. Only six seedlings were tried, and no root of these was rheotropic. The duration of the experiment was 48 hours, the roots elongating 1^{cm} to 2^{cm} in that period. The velocity of the current was 225^{cm} to 600^{cm} per minute.

Cucurbita pepo and *Citrullus vulgaris* grow primary roots very straight in an environment of water. Of the former species, forty-four seedlings have been used in five different experiments, in which the water temperature ranged from 17° to 23°, the velocity of current from 150^{cm} to 2000^{cm} per minute, and the duration of the experiments from 13.5 hours to 9 days. In none of these was any deviation from the vertical shown.

In *Citrullus vulgaris* thirty-one seedlings were employed in three experiments, the water temperature in two being 21° and in the third 24°. The revolution of water lasted in two for 17 hours, and for the third 24 hours. The velocity of current was from 100^{cm} to 1300^{cm} per minute. Only three slight positive curves were formed. In such a very slight result it may be assumed that the bending was not a response to the current, and hence *Citrullus vulgaris* may be accounted non-rheotropic.

Phaseolus vulgaris, *P. lunatus*, *P. multiflorus*, *Glycine hispida*, and *Dolichos lablab* have all shown themselves non-responsive to the flowing of water. The three species of Phaseolus and Dolichos produce many crooked roots in water; Glycine mostly straight roots. In all these experiments the contorted roots have been excluded from the results, and only those showing themselves straight after standing for 10 to 24 hours in still water were used subsequently in the flowing water. The smallest number of seedlings employed in any species was ten, and the largest forty-seven, with a total of 137. The water temperature in some cases was held constant throughout the experiment, and in others varied from 17° to 25°. The period ranged from 8 to 36 hours. Dolichos showed a very few roots inclined positively, and it is possibly rheotropic in a very low degree.

3. *Plants with a low degree of sensitiveness.*

It has already been intimated that the roots of the bulb of *Allium cepa*, and the primary roots of *Dolichos lablab*, may be slightly positively rheotropic. It is quite certain that the primary roots of the seedlings of *Vicia faba*, *Lathyrus odoratus*, *Lupinus albus*, and *Tropaeolum majus* are positively rheotropic, but only in a comparatively low degree. Juel, in several tests with seedlings of the small-seeded variety of *Vicia faba*, had trouble in controlling the Sachs's curvature. He obtained varying responses and a considerable number of non-responsive roots. He finally concluded that the roots were rheotropic, and bent more readily when so placed that the median plane of the seedling was parallel with the current rather than transverse.

My own experiments were not troubled with Sachs's curvature because of my method of securing the seedlings, and my results agree in a general way with those of Juel, though my plants were mostly of the variety known as "Windsor broad." Apparently, however, this variety is less responsive than that used by Juel, since, as will be seen, the Windsor broad shows many individuals as neutral, while it would be inferred from Juel's narrative that very few of his roots were neutral. Thus, among thirty-seven selected seedlings in four experiments with revolving basins of water, water temperature 19° to 23°, velocity of current 100^{cm} to 2500^{cm}, seventeen grew positively, three negatively, and seventeen were neutral. In two experiments, in each of which nine seedlings were suspended with their roots dipping into a brook of water in a wooded ravine in August, the average temperature being about 23°, all eighteen roots remained vertical, though increasing in length from 1^{cm} to 2^{cm} in the period. In the one experiment the period was 24 hours, and the velocity 450^{cm} per minute; in the other, the period was fourteen hours, and the velocity 900^{cm} per minute.

In a variety of *Vicia faba* with seeds 1.5^{cm} long and 1^{cm} broad, perhaps the same used by Juel, twelve seedlings were placed under experiment with the revolving basin, water temperature 21°, velocity 300^{cm} to 750^{cm} per minute, and period 24 hours. Six roots then showed positive curves from 15° to 90°, and the other six were vertical.

As to the relative degree of response shown by the seedlings when the median plane is parallel to the current of water and when the median plane is transverse, my results, and probably those of Juel, are too few to account as of great importance. In one experiment with six seedlings, with the median plane transverse to the current, four roots out of six responded positively, the greatest angle being 30°. In another experiment with ten seedlings, the median plane being parallel to the current, eight roots bent positively, two of them reaching an angle of 80°. In a third experiment with twelve roots, out of nine with the median plane parallel, four bent positively, while out of three with the median plane transverse, two bent positively. Thus it is shown that the root will respond to the water meeting it on any part of its circumference.

The low grade of responsiveness of *Vicia faba* to a current of water is shown not only in the fact of approximately 50 per cent. of the roots remaining neutral, but also in the exceedingly protracted latent period, and in the small angle attained in most curves. Thus in the experiment with the twelve seedlings of the small-seeded *Vicia faba* with a water temperature of 21°, no roots curved in the first 5 hours. In 8 hours four had curved positively, in 16 hours five had curved, and within the following 8 hours one more curved. Of the twenty-three positively curved roots in both varieties of *Vicia faba*, only three attained angles greater than 45° degrees from the vertical. The majority of curves were below 30°.

Lathyrus odoratus and *Lupinus albus* are, at least in some varieties, positively rheotropic. The latter was found rheotropic by Berg. Both these species produce fairly straight roots when growing in water. With water temperature from 21° to 24°

during a period of 24 hours, only three roots curved out of fifteen seedlings of mixed varieties of *Lathyrus odoratus*. In another group of twenty seedlings, in water temperature of 20° to 22°, only three or four weak curves showed after 24 hours, but fourteen good positive curves showed after 48 hours. Of the others, two were negative and four remained vertical. In a small-seeded variety of *Lupinus albus*, at a water temperature of 27°, sixteen seedlings in the revolving basins of water gave no curved roots during the period of 29 hours. A later experiment with a large-seeded variety, temperature in the water being 17° to 23° and the period 25 hours, gave twenty-two positively curved primary roots in a total of twenty-four. Each of the curves attained an angle of 45° or over. The velocities employed in the experiments with both these species extended from 50^{cm} to 500^{cm} per minute.

It is evident, therefore, that both these species have sensitive primary roots. Whether the varying sensitiveness observed was due entirely to the different varieties, or, in part, to temperature, to different seasons of the year, or to some other condition, was not determined. Enough testing was done to show that it was not due to difference in the water used in the experiments.

Tropaeolum majus behaves badly in water, 25 per cent. to 50 per cent. of the roots becoming contorted. In two experiments, with a total of thirteen straight roots, the period of revolution for one being 12 hours, and for the other 18 hours, the temperature of the water being 22° to 23°, and the velocities ranging from 225^{cm} to 625^{cm} per minute, no roots responded. In another experiment, same temperature, velocities from 100^{cm} to 900^{cm} per minute, twenty seedlings were used. No curve appeared for 6 hours; but at the end of 30 hours, fifteen of the primary roots were positive 15° to 19°, while the other five were pointing vertically downward. The secondary roots gave no certain response. There was considerable irregularity in the direction of growth, but, at the end of the period, the fifteen primary roots showed plainly that this species gives a rheotropic reaction.

4. *Plants with a high degree of sensitiveness.*

It has already been stated (p. 183) that in 134 individuals of four large-fruited varieties of Indian corn so many primary roots grew contorted in water that these plants are wholly unsuited for experiment. At the same time it is to be remembered that Jönsson, Berg, and Juel have found *Zea mays* rheotropic, though none of them states the variety used.

If instead of the large-fruited varieties of *Zea mays* we experiment with the dwarf *Zea mays*, with the white popcorn, we shall soon find this variety in its primary root highly sensitive to a current of water. Quite unlike the contorted roots of the field and sweet corn, the primary roots of the popcorn nearly all grow straight in water. In a total of seventy-nine seedlings in velocities of water of 25^{cm} to 1000^{cm} per minute, period 36 hours, and water temperature 19° to 23°, fifty-seven primary roots showed positive curves, six negative curves, and sixteen roots were neutral. A few of the negative curves were doubtless caused by the mechanical effect of the strongest current employed. The percentage of positive roots is here made but seventy-two, about the same as that of *Vicia sativa.* But many of the angles attained by the roots of the popcorn approximate 90° from the vertical, as shown in *fig. 3*. The general behavior of this seedling is so much better than that of *Vicia sativa*, that we are justified in according it a higher degree of responsiveness.

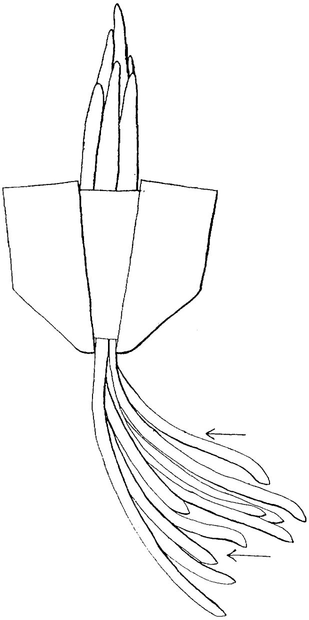

FIG. 3.—*Zea mays* (popcorn). End view of a row of ten seedlings after being in the water stream for 11 hours. The general direction of the roots is more than 45° from the vertical, and the tips of several are nearly 90° from the vertical. The drawing shows the actual size of the preparation, the seedlings growing from a wooden trough and being held in position by packing of cotton wool.

The Gramineae other than Zea, so far as studied, are also positively rheotropic. *Triticum vulgare* and *Secale cereale* were so determined by Jönsson, *Hordeum vulgare* and *Avena sativa* by Berg. In my experiments all four of these species were treated as already described for other plants. After the grains had been placed in the vertical position in sawdust, and there sprouted, they were secured in the vertical position, by means of strips of blotting paper and rubber bands, to the sides of wooden bars extending parallel with the diameter of cylindrical glass basins, and so placed that the lower ends of the grains just met the contained water. Here the preparation rested till the roots had attained a length of one or more centimeters. The revolution was then started. At once the question arises as to how these roots should be judged; for, as is well known, the roots of the cereals grow out in a bunch of several to many secondary members which do not all take the vertical direction till a considerable length is reached. The method finally found the most satisfactory was as follows: When a record was to be made the observer sighted horizontally along the row of roots, counting all roots positive whose apical portion deviated from a vertical plane in the direction against the stream, all roots negative that deviated from the vertical in the direction with the stream, and all roots neutral whose tips were in a vertical plane parallel with the row of seedlings. In placing the grains in position on the supports care was taken to arrange them so that about an equal number met the water current on the flanks, on the front, and on the back. Thus it would seem that there could be no objection to the method employed for judging of the rheotropism of these plants. An error in calling a root positively rheotropic that was only inclined against the stream because of its plagiotropic position would be counterbalanced by calling a root a negative that was inclined in the opposite direction, solely through its plagiotropism, provided the number of individuals employed was large. The results will show such a preponderance in favor of rheotropic response that there can be no question of the fact.

In *Triticum vulgare* ninety-three roots were observed, divided among three experiments. Temperature of the water was from 19° to 22°, velocity from 75^{cm} to 750^{cm} per minute (constant for any one root), period 24 hours for two experiments, and 48 hours for the third. Twenty-five roots were positive, three were negative, and sixty-five were neutral. The angles attained were not more than 20° from the vertical. This would seem to place the wheat among those of weak response to a current of water.

Secale cereale furnished sixty-two roots for observation, temperature of water 20° to 23°, velocity 100^{cm} to 1000^{cm} per minute, period of 15 hours. Fifty-nine roots were positive and three neutral. Several of the angles attained were 90°.

Hordeum vulgare had 102 roots under experiment in a water temperature of 20° to 22°, a velocity of 50^{cm} to 750^{cm} per minute, and periods of 7, 9, and 24 hours. Of positive roots there were eighty-four, negative seven, and neutral eleven.

Avena sativa was tested in five experiments with a total of 132 roots. The water temperature was 21° to 25°, the velocity of current 50^{cm} to 1000^{cm} per minute, and the period 9 hours to 33 hours. Ninety-seven roots bent positively, six negatively, and twenty-nine remained neutral. Many of the roots bent to an angle of 60°.

The four species of Gramineae just considered resemble one another in the production of good roots in water, in displaying positive rheotropism, and in producing a considerable percentage of neutral roots. The wheat shows the smallest number of responses of these four plants.

Of the Leguminosae, ten species have been studied, five being found non-responsive, and five responsive. All but the two most sensitive species have already received attention.

Vicia sativa was pronounced by Juel very sensitive to a stream of water. This author had not tried the much more sensitive Cruciferae. In my experiments *Vicia sativa* has proved itself relatively slow and weak in its response. It responds better than *Vicia faba*, but much less readily than a dozen other plants whose behavior is to be described later.

The experiments with *Vicia sativa* may be divided into two groups: those of a duration of 6 hours to 12 hours, and those of 48 hours. Forty-seven seedlings have had their roots stimulated by currents of water ranging in velocity from 150^{cm} to 750^{cm} per minute, water temperature 19° to 25°, period from 6 to 12 hours, giving twenty positive and twenty-seven neutral roots. Had the revolution of the basins of water been continued longer, it is certain that other roots would have become positive, as is shown by the following results: Eight seedlings had their roots subjected to the streaming of water in a revolving basin for 48 hours, water temperature 18° to 21°, velocity 450^{cm} to 500^{cm} per minute, giving seven roots positive and one negative. In another experiment, out of thirteen seedlings only two showed curves after 12 hours' revolution of the basin, while after another 12 hours ten roots had become positive. It is safe to assume that over 75 per cent. of the roots of *Vicia sativa* are responsive to the flowing of water, whereas only 50 per cent. of those of *Vicia faba* are responsive.

Both of these species are alike in the long duration of the latent period and in the smallness of the angle of curvature. It is certain that in my experiments with these two species, in a water temperature of 20° and an air temperature of 21.5° or higher, more than half the roots to respond rheotropically have shown the first curving later than 8 hours. Not 15 per cent. of those responding have shown a curve earlier than 6 hours. The greatest angle that any of my seedlings of Vicia has attained is 70°; the most of them have reached a deviation of 10° to 25°. *Fig. 4* shows a tracing from a photographic reproduction of the seedlings in one of the foreging experiments, and, with the restriction contained in the description accompanying the figure, is fairly representative of the behavior of this plant.

Pisum sativum resembles in its general behavior *Vicia sativa*. A number of its roots grow crooked in water, its latent period is long, and a considerable number of its roots are non-responsive. It shows, however, a higher percentage of curvatures in response to the stimulus, and the angle attained by the roots is greater than in *Vicia sativa*. In this series the temperature was kept constant throughout at 23° in air, almost the optimum for the growth of this species and variety; the velocity ranged from 50^{cm} to 1380^{cm} per minute and the period from 16 to 22 hours. Of the ninety-four roots used, seventy-four bent positively, ten negatively, and ten grew vertically. Of the seventy-four positive roots, sixty-one attained an angle between 45° and 90°; several reached 90°.

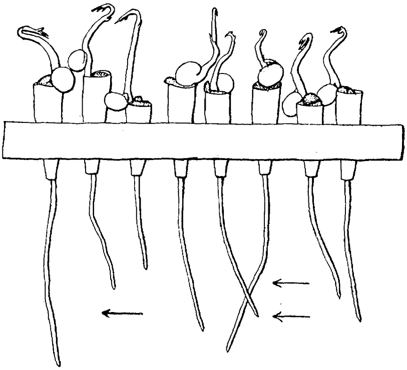

FIG. 4.—Tracing from a photograph, half natural size, of *Vicia sativa*. The seedlings were packed in glass tubes with cotton wool, and the tubes held in holes in a wooden bar. In order to secure a photograph to show the curves to best advantage, the bar was suspended parallel to the water-stream. It was found, however, that the resulting curves were not so great as when the row of seedlings extended, as usual, transversely to the stream. The smaller angles attained were probably due to the interference of the roots with the stream. This figure is presented principally for the purpose of comparing the sensitiveness of this species with that of *Raphanus sativus*, as shown in *figs. 6* and 7, page 198. As is not unusual in this species, the figure shows one root with a negative curve.

Among the Polygonaceae only *Fagopyrum esculentum* has been put under experiment. The primary roots of the buckwheat are evidently highly sensitive, but they show some inclination to form sudden curves in still water. Even though the roots grow irregularly in water, the contorted roots will bend their tips against a stream a short time after it is started. Twenty-six straight roots were selected for experiment. The temperature during the three experiments was respectively 21°, 18°, and 22° in the air. The velocity ranged from 75^{cm} to 750^{cm} per minute, and the periods were 24, 18, and 12 hours. Twenty-four roots became positive, and two negative. My notes record the angles of only seventeen of these twenty-six roots: thirteen bent positively to an angle of 90°, one to an angle of 15°, and two bent negatively to an angle of 90°. The last two, and perhaps some others, evidently curved, not because of the stream, but because of their objection to the water environment, whatever this objection may be. The relatively large number of positive roots, however, warrants us in concluding that this species is rheotropic.

Of the Compositae only *Helianthus annuus* has been used. Forty seedlings have been tested for a period long enough to determine their rheotropism. The temperature was 21° to 23° in air, the velocity 50^{cm} to 1000^{cm} per minute, the period 17 to 33 hours. Twenty-eight roots bent positively, six negatively, and seven were neutral. The roots bending positively did not attain as great an angle as those of Fagopyrum, less than one-half passing beyond 45°. The roots of Helianthus do not all grow straight in still water, and this behavior will account for the relatively large number of negative curves in the experiments.

The Cruciferae have furnished by far the best material for the study of rheotropism. Of the six species studied, five are rheotropic, only *Nasturtium officinale* showing itself wholly indifferent. The white mustard, the black mustard, the turnip, the cabbage, and the radish, but especially the first and the last of these five, give splendid examples of rheotropic roots. All of the Cruciferae tried produce straight roots in water. In size, the seedlings used were from 2^{cm} to 4^{cm} in length at the beginning of the experiment.

Brassica alba is one of the best of the eighteen species that have been found rheotropic. In five experiments with the revolving basins of water, in which fifty-one seedlings were used, with a velocity of 50^{cm} to 1000^{cm} per minute, a water temperature of 19° to 22°, and a period from 6 to 21 hours, forty-five roots bent strongly positively, the majority being over 45°, and many being 90°. Six roots were neutral. This gives a percentage of 88 and marks the white mustard as a remarkably good plant for experiment. Its great heliotropic sensitiveness requires that the experiments for rheotropism be carried on in the dark. *Fig. 5* shows the curves obtained in one experiment with this plant.

Brassica nigra responds more slowly than *Brassica alba* but attains almost as good a percentage, and almost as great angles. The sensitiveness of its roots to light requires that it, too, be kept in the dark in determining its rheotropism. Twenty-nine seedlings were used in two experiments with the revolving basins, the water temperature being 24°, the velocity 50^{cm} to 450^{cm} per minute, and the periods 9 hours and 15 hours. Twenty-four roots became positive and five remained neutral. In the experiment with the longer period, all of the roots that became positive, numbering fifteen, were 45° to 90° from the vertical. The result gives us 83 per cent of responsive roots.

Brassica campestris was tested in two experiments with a total of forty-two seedlings, water temperature 24°, velocity of current 60^{cm} to 560^{cm} per minute, period 24 hours, giving thirty-six positive curves averaging 45°, three negative curves, and three neutral roots. This gives a percentage of eighty-five positive roots. It will be noted that that the angle attained in these experiments is rather small. It may have been due to the rather high temperature. *Fig. 2* shows the result obtained in one experiment with this plant.

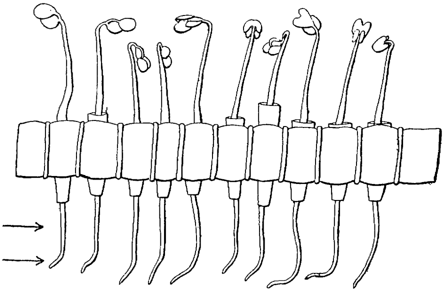

FIG. 5.—*Brassica alba.* A tracing from a photograph, three-fourths natural size. These seedlings were set in glass tubes in order to facilitate transfer for purposes of photographing. During the experiment the bar was held in a radius of the revolving basin for 18 hours, water temperature 21°, the range of velocities being 125^{cm} to 600^{cm} per minute. At the conclusion, the seedlings were twisted around through an arc of 90° in order to show their angles in the photograph. The figure is fairly representative, except that the tips declined slightly during the preparation for photographing.

Brassica oleracea was tested in two experiments, water temperature 24°, velocity 60^{cm} to 560^{cm} per minute, and period 20 hours. Thirty-four seedlings were used, of which thirty-two curved positively to an angle of 15° to 80°, while two curved negatively to an angle of 20°, giving a percentage of ninety-four positive roots.

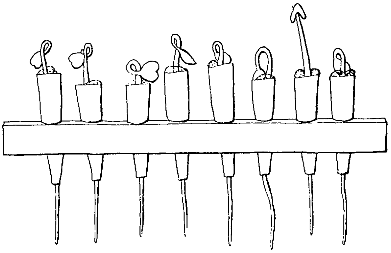

FIG. 6.—*Raphanus sativus* before the beginning of the experiment which gave the result in *fig.* 7. Tracing from photograph.

Raphanus sativus, the variety known as the "early long scarlet," has been for me the best of all plants for experiments with rheotropism. It is larger than any of the other Cruciferae worked with, and for that reason less liable to injury in handling. Its roots are insensitive to light, and hence experiments with it may be conducted in the general rooms of the laboratory. In the series described here, 140 seedlings have been used in nine experiments with the revolving basins of water. The water temperature has ranged from 20° to 25°, the velocity from 50^{cm} to 750^{cm} per minute, and the period from 5 to 33 hours. One hundred and twenty-three roots have bent positively, the majority from 45° to 90°; eight have bent negatively, and nine have grown vertically. The positive roots are, therefore, 87 per cent. The response of this plant to the water stream is relatively very ready. Two hours from the beginning, at a suitable temperature, well marked curves can be detected in 25 per cent. to 50 per cent. of the roots. The relative response of this plant and of *Vicia sativa* is well shown by comparing *figs.* 4 and 7.

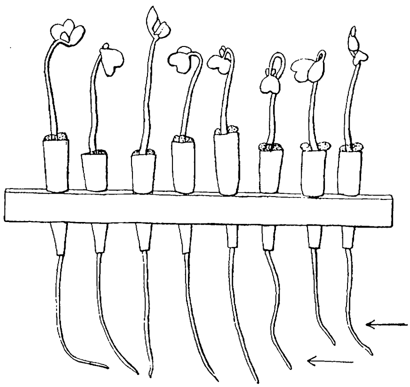

FIG. 7.—*Raphanus sativus*, tracing from a photograph. This figure is to be compared with *fig.* 4. The two give fairly well the relative response of *Vicia sativa* and *Raphanus sativus* in similar conditions. The experiments for both were carried on at the same time, the period of revolution being 23 hours, the temperature in water 19° to 22°, and the range of velocities 100^{cm} to 500^{cm} per minute. As stated under *fig.* 4, these preparations were made for photographing, and the curves are smaller than they would have been had not the bar of seedlings been held parallel with the stream of water.

[*To be continued.*]